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THE COMPARATIVE LEAF STRUCTURE OF THE STRAND PLANTS OF NEW JERSEY.

(PLATES II-V.)

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In the *Proceedings of the American Philosophical Society* for last year (XLVII: 97-110. 1908), I presented the results of my study of the leaf structure of the sand dune plants of Bermuda. So many points of interest developed in the course of that investigation, that I undertook a study of the leaf structure of the characteristic species growing along the sea shores of New Jersey. This investigation was also in part a continuation of those previously conducted on the geographic distribution of the New Jersey strand flora begun in 1892 and continued down to the present year.

PHYTOGEOGRAPHY OF THE STRAND.

The strand flora of New Jersey comprises several well-marked phytogeographic formations, namely, the sea beach formation, the dune formation, the thicket formation and the salt marsh formation. The sea beach formation comprises those plants which grow on the middle and upper beaches, the lower beach being wave swept. The typic plants of this formation are *Cakile edentula*, *Ammodenia* (*Arenaria*) *peplodes*, *Salsola kali*, *Euphorbia polygonifolia*, *Cenchrus tribuloides*, *Ammophila arenaria*, *Xanthium echinatum*, *Atriplex arenaria*, *Sesuvium maritimum*, *Strophostyles helvola* and *Solidago sempervirens*. The dunes of New Jersey consist of wind-blown silicious sand and occur at greater or less height along the entire coast from Sandy Hook to Cape May, while back of them occur salt marshes which fringe the open bays, or river channels. The character plants of the New Jersey dunes are the marram

grass, *Ammophila arenaria* (Plate II, Fig. 1), which anchors the sand, the beach pea, *Lathyrus maritimus*, *Hudsonia tomentosa* (Plate II, Fig. 2), *Solidago sempervirens*, *Euphorbia polygonifolia*, the wax berry, *Myrica carolinensis*, poison ivy, *Rhus radicans*, beach plum, *Prunus maritima*, and Virginia creeper, *Ampelopsis* (*Parthenocissus*) *quinquefolia*.

The thicket formation (Plate III, Fig. 3), as it exists on the New Jersey strand consists in some places entirely of shrubs, in other places, it is composed of trees which form a characteristic forest growth. The vanguard of this thicket consists of cedars, *Juniperus virginiana*, which never rise above the level of the dunes among which they grow. Young trees in the dune hollows are spire-shaped, but upon the tops reaching the general level of the dune summits, they become flat-topped and incline in a direction opposite to the prevailing wind. The following species enter into the thicket formation throughout coastal New Jersey: *Juniperus virginiana*, *Q. nana* (= *Q. ilicifolia*), *Q. lyrata*, *Q. obtusiloba* (= *Q. minor*), *Q. phellos*, *Pinus rigida*, *Sassafras officinale*, *Diospyros virginiana*, *Nyssa sylvatica*, *Acer rubrum*, *Magnolia glauca* (= *M. virginiana*), and as secondary species in the form of shrubs *Rhus copallina*, *Prunus maritima*, *Vaccinium atrococcum*, *V. corymbosum*, *Myrica carolinensis* and such lianes as *Vitis Labrusca*, *V. æstivalis*, *Ampelopsis quinquefolia*, *Rhus radicans* together with a host of herbaceous species mentioned in former papers.

Geographically there are two regions of salt marshes along the New Jersey coast, viz., that of the northern coast, north of the head of Barnegat Bay and that of the south and middle coast along Barnegat Bay and southward to Cape May. The salt marshes on the north coast are confined to the shores of the rivers which manage to cut their way through the sand barriers in order to reach the ocean. They are, therefore, comparatively circumscribed in area and are, as a rule, narrow strips bordering the tidal channels of the seaward-flowing streams. The salt marshes, however, south of Bay Head widen out into extensive expanses of flat, featureless character cut by numerous tidal channels (Plate III, Fig. 4). Those north of Barnegat Inlet nowhere exceed a mile in width, while south

of Barnegat Inlet the salt marshes widen out until in places they may be from two to four miles wide cut by thoroughfares into characteristic marsh islands. The tidal channels are generally bordered throughout the two regions by the tall salt grass, *Spartina stricta maritima*, back of which occur *Spartina patens*, *Juncus Gerardi* and *Distichlis spicata*. On the flat marsh only flooded to a depth of an inch or two at high tide occur *Limonium carolinianum*, *Plantago maritima*, *Aster subulatus*, *Suaeda linearis*, *Distichlis spicata*, *Chenopodium rubrum*, *Pluchea camphorata*, *Salicornia herbacea*, *S. mucronata*, *Tissa marina* and *Gerardia maritima*, while *Baccharis halimifolia* and *Hibiscus moscheutos* occur in salt marsh soil which is never flooded with each rising tide. *Eleocharis pygmaeus* forms floating mats in the sloughs surrounded by salt marsh at Sea Side Park (Plate III, Fig. 4).

ECOLOGIC FACTORS.

The ecologic factors must be considered under two heads, because the strand plants are found growing under two distinct environmental conditions. The typic strand plants display various xerophytic adaptations to their growth in the silicious sand of the sea beaches and sand dunes. The factors which are instrumental in producing the xerophytic structures which the leaves of strand plants show may be considered to be the following: (1) The permeability of the sand to water, so that after a rain the surface layers dry out. (2) The action of strong winds that blow across the sandy beaches increasing the rate of transpiration materially and carrying sand, which is directed against the plant, as a sand-blast. (3) The relatively dry soil and the increased transpiration by wind action necessitates the adoption of structures which will enable the plant to conserve its water supply. (4) The reflection of light from the sand and the foam-crested breakers beyond is influential, but this influence is not so marked as in Bermuda where the sand is a white coral sand and presumably the sunlight is reflected to a greater extent. (5) The illumination from above has also been effective, but perhaps not so much so as in Bermuda. (6) The action of the salt spray blown inland by the wind is

effective in modifying the structure of the beach and dune plants, but is hardly active upon the species of the thicket formation. (7) Formerly it was supposed that the plants of the sea beaches had to contend against the salt content of the soil, but Kearney has shown that the amount of salt in the sand of sea beaches is a negligible quantity, as many agricultural soils of the interior contain relatively more salt than the seashore sand.

While the beach plants have, therefore, according to the researches of Kearney, been removed from the list of true halophytes, nevertheless the typic salt marsh species show marked halophytic adaptations and belong to the second category of strand plants. The most potent factor which is here influential is the presence of free salt water about the bases and roots of the salt marsh plants. It was pointed out by Schimper that any considerable amount of salt in the cell sap is detrimental to the plant and that here we have the probable cause of the characteristic halophytic modifications which aim, therefore, at decreasing the amount of water transpired. To this Warming replied, that even if transpiration were diminished, slowly, but surely, an amount of salt would accumulate in the plant which would prove its destruction. On the other hand, Warming proposed that the protective contrivances against strong transpiration are necessary in halophytes, because absorption of water from a salt solution is slow and difficult and what water the plant had absorbed must be conserved in order to provide against desiccation, while the plant is absorbing enough water to replace that lost in ordinary transpiration. Sodium chloride in solution is known to have strong plasmolytic properties, removing water from living cells when subjected to its action. Ganong has found that the root hairs of *Salicornia herbacea*, a typic halophyte, can endure a 100 per cent. sea water without plasmolysis; those of *Suaeda maritima* 80 per cent.; those of *Plantago maritima* 70 per cent.; while those of *Atriplex patulum* withstood 50 per cent. sea water. Graves found that the root hairs of *Ruppia maritima* could stand a 105 per cent. sea water with occasionally very slight plasmolysis, while with 110 per cent. sea water, it was rather slow, but finally distinct. So that the group of halophytes with which we are here dealing

possesses great power of resisting the action of sodium chloride in solutions as strong, as sea water. This is reflected in their structure.

STRUCTURAL ADAPTATIONS.

These will be treated as applicable to the strand plants, as one category, and to the salt marsh plants as the other.

Strand Plants.—The leaf adaptations to light are found in the increased number of palisade layers, their presence on the upper and under sides of the leaves and their arrangement, so that the central part of the leaf becomes palisade throughout. When both leaf surfaces are equally illuminated, the leaf may be termed isophotic, when unequally illuminated, diphotic. Diphotic leaves which show a division into palisade and spongy parenchyma have been called by Clements diphotophylls. Isophotic leaves are of three types, viz., the staurophyll, or palisade leaf; the diplophyll, or double leaf; the spongophyll, where the rounded parenchyma cells make up the bulk of the leaf in cross-section. Succulent leaves are those developed for water storage and to some extent the presence of latex provides against desiccation. The depression of the stomata, the development of a thick cuticle, the presence of a hypodermis of thick-walled cells, the presence of hairs and the formation of air-still chambers by a folding of the leaf tissue are all structures which assist in the regulation of transpiration. The following is a classification of the different leaf structures with reference to the strand plants which illustrate such adaptive arrangements.

Thick Cuticle: *Ammophila arenaria*, *Quercus obtusiloba*, *Ilex opaca*.

Thick Epidermis: *Baccharis halimifolia*, *Ampelopsis quinquefolia*, *Euphorbia polygonifolia*, *Cakile edentula*.

Hypodermis Present: *Ammophila arenaria*.

Two or More Rows of Palisade Cells: *Lathyrus maritimus*, *Strophostyles helvola*, *Ampelopsis quinquefolia*, *Quercus obtusiloba*, *Vitis Labrusca*, *Ilex opaca*, *Baccharis halimifolia*.

Stomata Depressed (slightly): *Euphorbia polygonifolia*, *Lathyrus maritimus*, *Ilex opaca*, *Hudsonia tomentosa*; (deeply) *Ammophila arenaria*, *Lathyrus maritimus* (Sea Side Park), *Atriplex hastata*, *Vitis Labrusca*.

Succulent Leaf: *Cakile edentula*, *Solidago sempervirens*, *Atriplex hastata*.

Leathery Leaf: *Lathyrus maritimus*, *Ampelopsis quinquefolia*, *Quercus obtusiloba*, *Xanthium echinatum*, *Ilex opaca*.

Wiry Leaf: *Ammophila arenaria*, *Cenchrus tribuloides*,

Hairy Leaf: *Ammophila arenaria*, *Xanthium echinatum*, *Quercus falcata*, *Hudsonia tomentosa*, *Vitis Labrusca*, *V. æstivalis*, *Cenchrus tribuloides*.

Leaf Surface Papillate: *Euphorbia polygonifolia*.

Leaf Becoming Erect in Sun Position: *Strophostyles helvola*, *Lathyrus maritimus*, *Euphorbia polygonifolia* (leaf blade folding along the midrib).

Overlapping Leaves: *Hudsonia tomentosa*.

Latex Tissue: *Euphorbia polygonifolia*.

Raphides: *Vitis æstivalis*, *V. Labrusca*.

Sphærocrystals: *Atriplex hastata*, *Ilex opaca*.

Idioblasts: *Cenchrus tribuloides*.

Diplophyll: *Euphorbia polygonifolia*, *Strophostyles helvola*, *Lathyrus maritimus*, *Ampelopsis quinquefolia*, *Quercus obtusiloba*, *Q. falcata*, *Vitis Labrusca*, *V. æstivalis*, *Ilex opaca*, *Baccharis halimifolia*.

Diplophyll: *Cakile edentula*, *Atriplex hastata* (Belmar), *Xanthium echinatum*.

Staurophyll: *Atriplex hastata* (Normandie), *Solidago sempervirens*.

Spongophyll: *Hudsonia tomentosa*, *Cenchrus tribuloides*.

Salt Marsh Plants.—The majority of the salt marsh species studied showed two marked characteristics, namely, succulency and wiriness. The following is a categoric presentation of the structure of their leaves. The smooth character of the leaves will be noted with the exception of *Gerardia maritima*, *Hibiscus moscheutos*, *Pluchea camphorata* which grow back in the interior of the salt marshes away from the tidal water.

Thick Cuticle: *Spartina stricta maritima* (lower surface).

Thick Epidermis: *Distichlis spicata* (lower surface), *Aster*

subulatus, *Suæda linearis*, *Gerardia maritima*, *Limonium carolinianum*.

Hypodermis Present: *Spartina stricta maritima*, *Distichlis spicata*.

Two or More Rows of Palisade Cells: *Aster subulatus*, *Limonium carolinianum*, *Gerardia maritima*, *Hibiscus moscheutos*.

Stomata Depressed: *Spartina stricta maritima*, *Tissa marina*, *Plantago maritima*, *Aster subulatus*, *Chenopodium rubrum*.

Hairy Leaf: *Gerardia maritima*, *Hibiscus moscheutos*, *Pluchea camphorata*.

Succulent Leaf: *Tissa marina*, *Plantago maritima*, *Aster subulatus*, *Suæda linearis*, *Chenopodium rubrum*, *Limonium carolinianum*.

Wiry Leaf: *Spartina stricta maritima*, *Distichlis spicata*, *Gerardia maritima*.

Leathery Leaf: *Hibiscus moscheutos*, *Pluchea camphorata*.

Diphotophyll: *Aster subulatus* (drawing is upside down), *Limonium carolinianum*, *Gerardia maritima*, *Hibiscus moscheutos*.

Diplophyll: *Tissa marina*, *Suæda linearis*.

Staurophyll: *Chenopodium rubrum*.

Spongophyll: *Plantago maritima*, *Pluchea camphorata*.

DETAILED STRUCTURE OF THE LEAVES.

The sections of the leaves which were studied were made free-hand with a razor, stained with Bismarck Brown and mounted for permanency in Canada Balsam. The drawings of these sections were made by the use of the micro-projection electric lantern, so that in every case (32 leaves) the sections were enlarged to the same extent and therefore the drawings were made on the same scale. The details of leaf structure and those of the stomata were made from a microscopic study after the main features of the leaf structure had been located by the micro-projection lantern. In this way the relative size of each leaf section is maintained in the thirty-two detailed drawings presented in the accompanying two plates (Plates IV and V). The drawings of stomata were not made to scale.

Strand Plants.—The typic sand-inhabiting plants will be described first.

Ammophila arenaria (Plate II, Fig. 1; Plate IV, Figs. 1, 1a, 2, 2a).—The beach, or marram grass, is a perennial species with firm, running rootstocks, which on account of their length, and the readiness with which the rigid, leafy culms arise from them serve to bind the drifting sand. The one-flowered spikelets are crowded in a long spike which reaches its full development in August and September. The leaves are involute and in a Wildwood-grown specimen (Plate IV, Fig. 1) examined microscopically the lower epidermis consisted of small cells with thick outer wall reinforced by 2–3 rows of hypodermal sclerenchyma isolated in patches below the vascular bundles. The upper epidermis, covering the grooves and the ridges, is irregular owing to the development of short, sharp-pointed hairs like canine teeth, which help to form an air-still chamber. The stomata are much depressed and level with the lower wall of the epidermal cells (Plate IV, Figs. 1a and 2a). Beneath the epidermis, hypodermal sclerenchyma is found in several well-marked rows. The chlorenchyma occupies a position on either side of the veins which run lengthwise. In the leaf section of a plant gathered at South Atlantic City (Plate IV, Fig. 2), the lower epidermis is reinforced by a continuous band of hypodermal sclerenchyma. The hypodermal sclerenchyma in the upper part of the ridges is more abundant than in the Wildwood-grown plants. A section of a leaf from a plant that grew on the low dunes of Belmar had comparatively little hypodermal sclerenchyma and in every way it was a thinner leaf than those from the Wildwood and South Atlantic City specimens.

Euphorbia polygonifolia (Plate IV, Figs. 3 and 3a).—The sea-side spurge is a prostrate, spreading herb, with oblong-linear leaves slightly cordate, or obtuse at the base and folding together along the midrib. The most conspicuous feature in the section is the large latex canals which fairly fill the center of the leaves and are marked by large surrounding, secreting cells. The upper epidermal cells are papillate, and the lower epidermal cells are without these papillæ, but the outer wall is thickened. The stomata are slightly

depressed (Plate IV, Fig. 3a). The loose parenchyma is prominent, as also the single row of palisade cells.

Strophostyles helvola (Plate IV, Figs. 4 and 4a).—This annual, trailing, leguminous herb has ovate to oblong-ovate leaflets with a more or less prominent rounded lobe toward the base. The flowers produced from June to September are greenish-white to purplish. In the hot sun, the leaflets assume hot-sun positions. The cells of the upper epidermis are thin-walled with the outer wall slightly thickened. Two well-marked rows of palisade cells are present, while the stomata are at the surface (Fig. 4a). The loose parenchyma is clearly seen and the lower epidermis consists of thin-walled cells.

Lathyrus maritimus (Plate IV, Figs. 5, 5a, 7, 7a).—The beach pea is a perennial, stout, trailing plant, as it occurs on the dunes of New Jersey. The coarsely toothed stipules are nearly as large as the leaflets, which are 6–10 in number, ovate-oblong. The leaflets assume hot-sun positions, especially those near the surface of the sand. The flowers are large and purplish, appearing from June to September. The epidermal cells on both the upper and lower surfaces of the leaflets are thin-walled with a slightly thicker outer wall, rounded, almost chain-like in arrangement. The loose parenchyma is compact and there are two rows of palisade cells.

Cakile edentula (Plate II, Fig. 1; Plate IV, Figs. 6 and 6a).—The sea rocket is a fleshy annual growing on the upper sea beaches and in clumps on the sand dunes (Plate II, Fig. 1). Its fleshy leaves are obovate, sinuate and toothed. The epidermal cells are large with outer walls slightly thickened, while the parenchyma cells are large and directed vertically with the exception of a few central cells, so that the leaf structure is that of a typic diplophyll. The stomata are at the surface (Fig. 6a). The xerophytic structure is, therefore, seen in the fleshy character of the leaf and in the arrangement of the internal parenchyma cells.

Solidago sempervirens (Plate IV, Figs. 8 and 8a).—The seaside golden-rod is a smooth, stout plant 0.3–0.5 m. high. The somewhat fleshy leaves are entire, lanceolate, slightly clasping; the lower ones are oblong-lanceolate, obscurely triple-nerved and all of the leaves

are vertical or nearly so. The contracted panicle of heads appears from August to November. The thin-walled, upper epidermal cells are approximately square in outline in the transverse view, only the outer wall being somewhat thickened. Chlorenchyma cells almost homogeneous, are directed vertically, hence the leaf is a staurophyll.

Atriplex hastata (= *A. patula* var. *hastata*) (Plate IV, Figs. 9, 9a, 10 and 10a).—The orache is an erect, or spreading, stout plant and at least the lower leaves are broadly triangular, hastate, often coarsely and irregularly toothed. The upper and lower epidermal cells are large, thin-walled. The chlorenchyma of similar elongated cells extends from the upper to the lower surface, so that the leaf is a typic staurophyll. Large sphærocrystals are present in the parenchyma cells of the leaf and the guard cells of the stomata are considerably sunken beneath the surface (Figs. 9a and 10a). The leaves of the specimen from Belmar were somewhat thinner than those from Normandie and the chlorenchyma cells were more rounded.

Hudsonia tomentosa (Plate II, Fig. 2; Plate IV, Figs. 11, 11a).—The dunes are in many places covered with this heath-like plant (Plate II, Fig. 2), which is an important sand binder, as it grows in dense clumps. The small awl-shaped leaves are oval or narrowly oblong and are close-pressed and imbricated, covered with a downy tomentum. The epidermal cells of the leaves are thin-walled and covered with slender, sharp-pointed hairs with a smooth cuticle. The hairs are so numerous on both sides of the leaf, that they act effectively in controlling transpiration. The guard cells of the stomata are only slightly depressed (Fig. 11a).

Cenchrus tribuloides (Plate IV, Figs. 12, 12a and 12b).—The sand bur grass branches extensively and sometimes has the trailing habit. The blades are more or less involute, owing to the presence of bulliform cells. The upper epidermal cells are marked by crystalline idioblasts (Fig. 12a) in an elongated form like the cystoliths in the leaf of the rubber plant, *Ficus elastica*. The epidermal cells on the under side of the leaf where the sclerenchyma occurs are terminated by short cusp-like spines. The guard cells (Figs. 12b

and 12c) are not sunken below the general surface. The upper epidermal cells are large, irregular in size and rounded. The lower epidermal cells are irregular and consist of bulliform with spiny hair cells opposite the leaf veins. The leaf exhibits a typical spongo-phyll structure.

Xanthium echinatum (Plate IV, Figs. 13 and 13a).—The cockle bur has broadly ovate, cordate leaves and the whole plant is rugose, especially the leaf surfaces. The upper and lower epidermal cells are thin-walled and provided with stout, projecting, multicellular hairs. The palisade cells extend through the leaf except a narrow row of cells near the center. Although this leaf has been classified as a diplophyll, yet it might with equal propriety be called a staurophyll.

Quercus obtusiloba (Plate IV, Fig. 14).—The post oak is a common tree in the pure dune sand of the New Jersey coast. The leaves are obovate in outline, 1–2 dm. long, the usually fine lobes spreading, the middle pair of sinuses are deep, wide and obliquely rounded at the bottom of the lobes. The leaves are leathery, thick and shining with scattered hairs above, densely gray, or yellowish hairy beneath. The epidermal cells are small with thick cuticle and the lower surface shows the presence of multicellular hairs. The palisade rows number from two to three and the loose parenchyma is compact. The leaf is a typical diphotophyll.

Quercus falcata (Plate IV, Figs. 15 and 15a).—The Spanish oak has leaves which are prolonged into a more or less scythe-shaped lobe with the under leaf surfaces grayish-downy or fulvous. The upper epidermal cells are large and thin-walled, as are also the lower epidermal cells. From the lower surface, a lot of compound hairs project, the tines of which are straight, sharp-pointed cells. The stomata are not depressed and a single row of palisade cells is present, so that the leaf is a typical diphotophyll.

Vitis Labrusca (Plate IV, Figs. 16 and 16a).—The northern fox grape has large leaves which are entire, or deeply lobed, slightly dentate. They are rusty-wooly beneath. The vines begin their growth on the forest trees, and as the sand drifts in around them, the grape vine branches grow out in a prostrate manner over the

surface of the dune sand. The upper epidermal cells are thin-walled. The palisade layer consists of one row of cells and below it we find cells here and there containing a mucilaginous substance in which are imbedded raphides, or needle-shaped crystals. The loose parenchyma is prominent and the lower epidermal cells are thin-walled and from them grow out long unicellular, sharp-pointed, straight hairs which become matted together. This hairy covering is of use in the regulation of transpiration. The guard cells are somewhat depressed (Fig. 16a) and the leaf exhibits a typical diphotophyll structure.

Vitis æstivalis (Plate IV, Fig. 17).—The summer grape has large unlobed or more or less deeply and obtusely 3-5-lobed leaves, provided with a very wooly and mostly rust-red, or tawny-flocculent tomentum. This tomentum does not appear in the section, because the wooly hairs are mostly attached to the veins beneath and merely cover the epidermal surface between, so that a section which does not include the veins does not show the hairy covering of the under side of the leaf. The upper and lower epidermal cells are thin-walled and in the single palisade layer are found cells containing a mucilage in which are imbedded raphides, or needle-shaped crystals of calcium oxalate.

Ilex opaca (Plate III, Fig. 3; Plate IV, Figs. 18 and 18a).—In the reproduced photograph (Plate III, Fig. 3), the holly is found associated with *Sassafras officinale*, *Rhus radicans* and *Solidago sempervirens*. The leathery oval, spiny-margined holly leaves have an upper epidermis of small cells covered with an extremely thick cuticle. Three rows of palisade chlorenchyma are present and a loose parenchyma, as an area of considerable width with large intercellular lacunæ. The lower epidermis consists of thick-walled cells and the guard cells, if sunken, are only depressed to the extent of the thick cuticle. Sphærocrystals are present in some of the cells of the third palisade row of cells. A tree with spineless-margined leaves was formerly found on the dunes at South Atlantic City. The leaf is a typical, xerophytic diphotophyll.

Baccharis halimifolia (Plate IV, Figs. 19 and 19a).—The leaves of the groundsel bush are thickish, vertical and obovate to wedge-

shaped, coarsely toothed, or the upper leaves entire. The upper epidermal cells have a considerably thickened outer wall with a warty cuticle. Stomata occur on both leaf surfaces with their guard cells not depressed below the surface. Palisade chlorenchyma of two rows of cells extends to the centrally placed bundles of the leaf and it is rather openly arranged. The loose parenchyma with large spaces shows its cells generally directed in a vertical manner, suggesting a staurophyll, but the bifacial structure is clearly recognizable, so that we may classify the leaf as a diphotophyll. The lower epidermis of thin-walled cells shows a roughened outer cell wall surface.

Ampelopsis quinquefolia (Plate IV, Figs. 20 and 20a).—The Virginia creeper with a compound leaf with five leaflets is an element of the dune flora of New Jersey. It begins to ascend forest trees, and if these trees are surrounded by drifting sand, the vine spreads out over the sand surface. In other places, it grows on the surface of the dunes and helps to bind the wind-blown sand. The sand-grown plants have leathery leaves in which the upper epidermal cells are compact with the outer wall thickened and its surface rugose. Two rows of palisade cells may be found and the loose parenchyma occupies the other half of the leaf below the midrib and the veins. The stomata are not sunken, and the leaf is a typic diphotophyll.

Salt Marsh Plants.—The plants of this group are all of them true halophytes, and at the conclusion of the description which follows of the histology of their leaves, a comparison will be drawn between their leaf structure and that of the leaves of the sand strand plants previously described.

Spartina stricta maritima (= *S. glabra*) (Plate V, Figs. 21 and 21a).—The salt marsh grass is a tall species 0.6–2.4 m. high, leafy to the top and growing along the shore in pure salt water. The leaves are 5–7 dm. long, 1–1.5 cm. wide, usually flat, but sometimes involute. The lower epidermal cells are strongly cuticularized, and where the bundles occur they are reinforced with hypodermal sclerenchyma. The upper leaf surface is raised into ridges, which are covered with small cuticularized epidermal cells without hairs, while

the stomata found near the bottom of the grooves have their guard cells depressed below the surface (Fig. 21*a*). Bulliform cells are absent. The chlorenchyma is radially arranged on each side of the bundles, while the parenchyma sheath surrounding the bundles also contains some chlorophyll.

Distichlis spicata (Plate V, Fig. 22).—The spike grass, or alkali grass, occurs in the salt marshes along our eastern coast from Nova Scotia to Texas, along the Pacific coast and in alkaline soil through the interior to the Rocky Mountains and southward in alkali sinks into Mexico. The culms are 1.5–6 dm. high and the leaf blades are often conspicuously distichous, rigidly ascending. The lower epidermis consists of thick-walled cells, the outer wall being especially thick. The upper epidermis consists of projecting hair cells with thick walls resembling in shape a canine tooth and found covering the ridges down into the grooves between, so that an air-still chamber is formed. The bundles are surrounded with thick-walled cells, which are in turn engirdled by a parenchyma sheath, while the rest of the leaf section is occupied by chlorenchyma.

Tissa marina (= *Buda marina*, *Spergularia salina*, *Spergularia marina*) (Plate V, Figs. 23 and 23*a*).—The sand spurrey is a much-branched, procumbent, or suberect, annual herb more or less distinctly fleshy. The leaves are linear and terete surrounded with large, thin-walled, epidermal cells with several rows of palisade parenchyma directly beneath and completely surrounding the large thin-walled parenchyma cells of the interior. The stomata are depressed below the surface (Fig. 23*a*). A typic, succulent diplophyll.

Plantago maritima (= *P. decipiens*) (Plate V, Figs. 24 and 24*a*).—The seaside plantain has linear to nearly filiform leaves 1–10 mm. broad, indistinctly ribbed and fleshy. The epidermal cells are large thin-walled with the outer wall slightly thickened with minute projecting points. Palisade cells are entirely absent and large parenchyma cells with chlorophyll fill the interior, extending to the bundles placed near the center. The stomata are not depressed, or only slightly so (Fig. 24*a*).

Aster subulatus (Plate V, Figs. 25 and 25*a*).—The leaves of the salt marsh aster are linear-lanceolate and pointed. The upper

leaf surface (turned upside down in Fig. 25) consists of thick-walled epidermal cells beneath which are two rows of illy defined, palisade cells, while beneath the palisade are compactly-placed, rounded chlorenchyma cells extending to the loose parenchyma cells with large intercellular spaces. The lower convex, epidermal surface is composed of thick-walled cells, the outer wall being especially thick. The guard cells are depressed the thickness of the outer cell wall (Fig. 25a).

Limonium carolinianum (Plate V, Figs. 26 and 26a).—The sea lavender has thick, stalked, radical leaves from which the much-branched scape arises, bearing small, lavender-colored flowers. The epidermal cells are large, thin-walled, but the outer wall is slightly thicker than the other walls. Two rows of palisade cells are found and a spongy parenchyma of rounded cells. The stomata are at the surface (Fig. 26a).

Suaeda linearis (Plate V, Fig. 27).—The sea blite is an erect, or ascending, fleshy, saline plant 2–9 dm. high. Its leaves are narrowly linear and acute. The epidermal cells are thin-walled, but project as rounded knobs the tops of which are thickened. The chlorenchyma, as palisade tissue, is found equally developed on the upper and the lower surfaces, while the interior cells are large and rounded parenchyma elements. A typical diplophyll.

Gerardia maritima (Plate V, Figs. 28 and 28a).—This marsh plant is a slender, erect, branching annual, somewhat fleshy with linear, obtuse leaves. The upper leaf epidermis has two kinds of hairs, straight, projecting ones and low, dome-shaped hairs, the terminal cells containing a brown substance. The palisade chlorenchyma forms two well-defined rows with compact spongy parenchyma beneath. The lower epidermis consists of thin-walled cells with superficial guard cells (Fig. 28a).

Chenopodium rubrum (Plate V, Figs. 29 and 29a).—The coast blite has a much-branched, angled stem with thickish, triangular, lanceolate leaves tapering below into a wedge-shaped base and above into an acute point, sparingly and coarsely toothed. The epidermal cells are thin-walled, with the outer wall curved outward. The vascular bundles are centrally placed, while the elongated, rounded

chlorenchyma cells are aligned as palisade. Sphærocrystals are abundant and the guard cells are depressed considerably (Fig. 29a).

Hibiscus moscheutos (Plate V, Figs. 30 and 30a).—The swamp rose-mallow is a tall perennial with showy rose pink, pink or white flowers and alternate ovate, pointed leaves, sometimes 3-lobed with a downy, whitened, under surface. The upper epidermal cells are comparatively thin-walled, while the lower epidermis of thin-walled cells is characterized by clusters of long, straight, pointed hairs densely matted together. There are two rows of palisade cells beneath which is found spongy parenchyma, while the guard cells of the stomata are slightly raised above the general epidermal surface (Fig. 30a). The leaf is a diphotophyll.

Pluchea camphorata (Plate V, Figs. 31 and 31a).—The salt marsh fleabane is an annual with oblong-ovate, or lanceolate, slightly petioled leaves. The stem and leaves are somewhat glandular, emitting a strong, or camphoric, odor. The epidermal cells are thin-walled and multicellular hairs abound on both surfaces. The stomata are not depressed (Fig. 31a). The chlorenchyma in the form of rounded cells is not differentiated into palisade and spongy parenchyma. A spongophyll.

Eleocharis pygmæa (= *E. nana*) (Plate V, Figs. 32 and 32a).—This small sedge formed small floating masses on the surface of the salt water sloughs at Sea Side Park (Plate III, Fig. 4): The bristle-like culms are tufted at the base and in section show large air canals, or lacunæ, surrounded by small thin-walled parenchyma cells. The bundles are reduced in size and the epidermis is composed of small thin-walled cells. A typic hydrophyte adapted to an halophytic existence.

GENERAL CONCLUSIONS.

We have listed twenty plants among those which grow on the sand strand and eleven which may be considered to be typic salt marsh species. Out of the twenty strand plants four are succulent, or twenty per cent., while out of eleven salt marsh species six are succulent, or over fifty per cent., so that the salt marsh species are preponderantly succulent. Only three of the salt marsh plants studied have epidermal hairs, while nine of the strand plants

are hairy. Eleven of the strand species are diphotophylls, and of these six have two rows of palisade chlorenchyma. Only four of the salt marsh species are diphotophylls, and each of them has two palisade rows. Reference to the classification of sand strand and salt marsh species given above will enable the student to pick out other differences existing between the sand strand and the salt marsh species, as regards their leaf structure.

BIBLIOGRAPHIC NOTES.

Little has been done in America to study the influence of environment upon the internal structure of plants, but a start has been made and it is only a matter of time when a large amount of important data will have been collected for comparison and generalization. As bearing upon the study of the sea strand vegetation may be mentioned the following papers. Kearney has discussed in his paper, "The Plant Covering of Ocracoke Island: A Study in the Ecology of the North Carolina Strand Vegetation" (Contributions U. S. National Herbarium, V: 280-312), the histologic structure of plants found upon Ocracoke Island as sand strand and salt marsh species. In this paper the following plants concern us: *Spartina stricta*, *Tissa marina*, *Solidago sempervirens*, *Aster subulatus* and *Baccharis halimifolia*. In a second paper, "Report on a Botanical Survey of the Dismal Swamp Region" (Contributions U. S. National Herbarium, V: 484-509), under anatomic notes, Kearney discusses the leaf structure of some selected plants. None of these plants actually concern this paper, except *Pluchea fætida* and *Baccharis halimifolia*. Edith Schwartz Clements, in a thesis submitted to the faculty of the Graduate School of the University of Nebraska for the degree of doctor of philosophy (June, 1904), gives a useful historic résumé of the study of leaf structure from an ecologic standpoint and also considers in a detailed manner the structure of about three hundred species collected in the Colorado foothills and mountains of the Pikes Peak region of the Rocky Mountains with reference to the surrounding physical factors, which were determined by careful instrumental readings. Lastly, Harshberger, in a paper noticed above, discusses the leaf structure of some seventeen



FIG. 1.



FIG. 2.



FIG. 3.

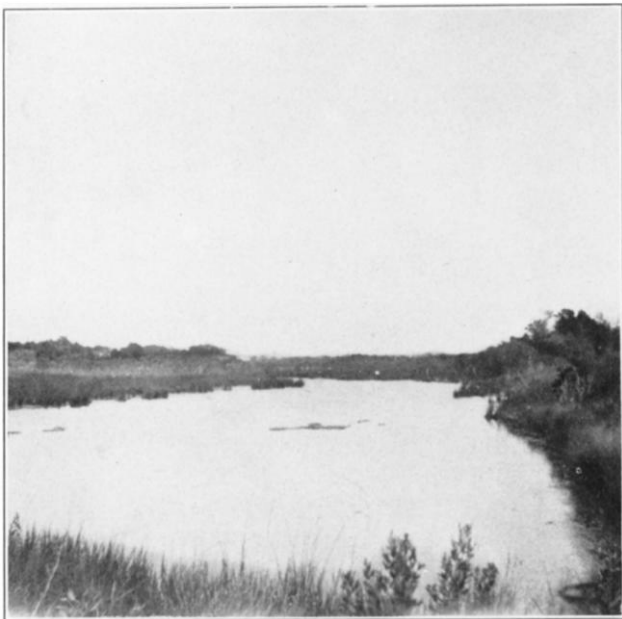
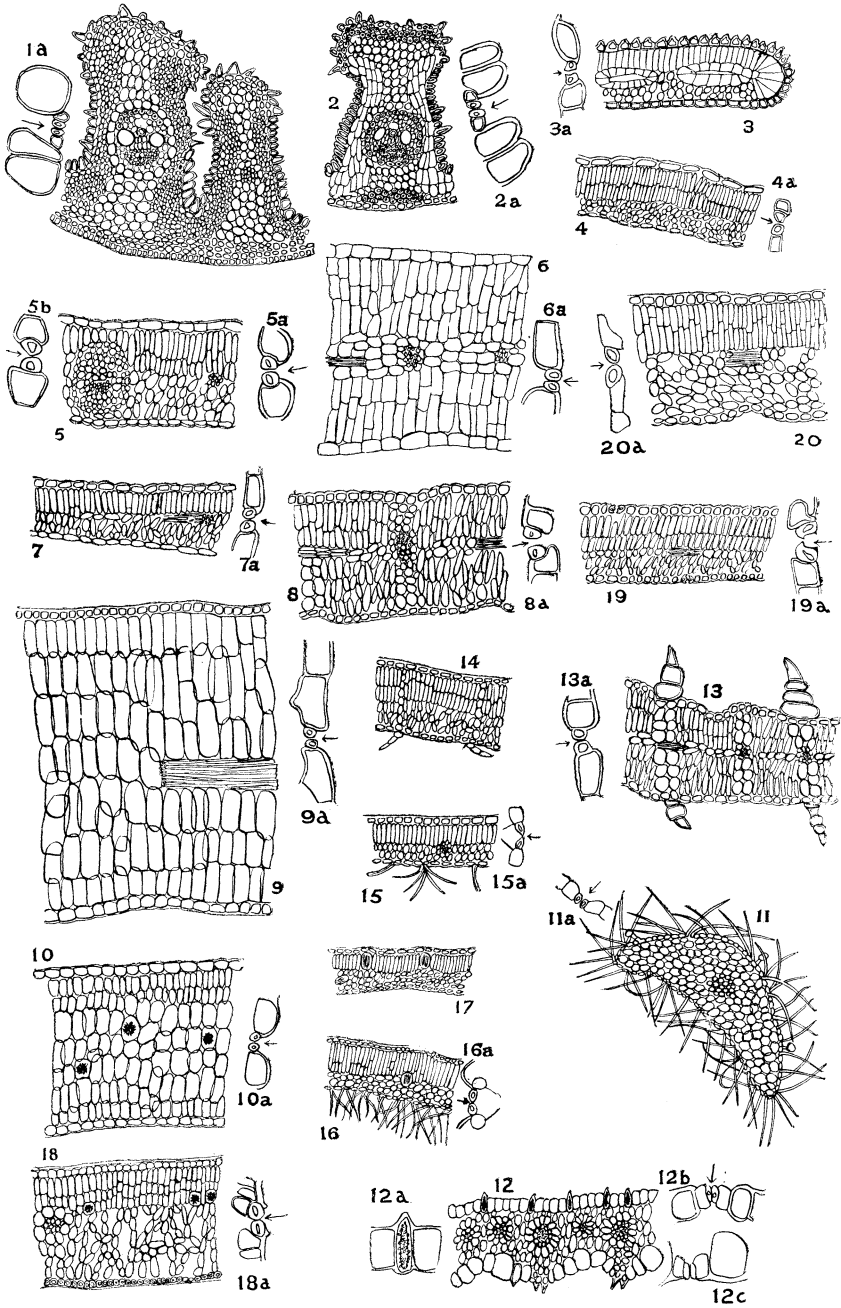
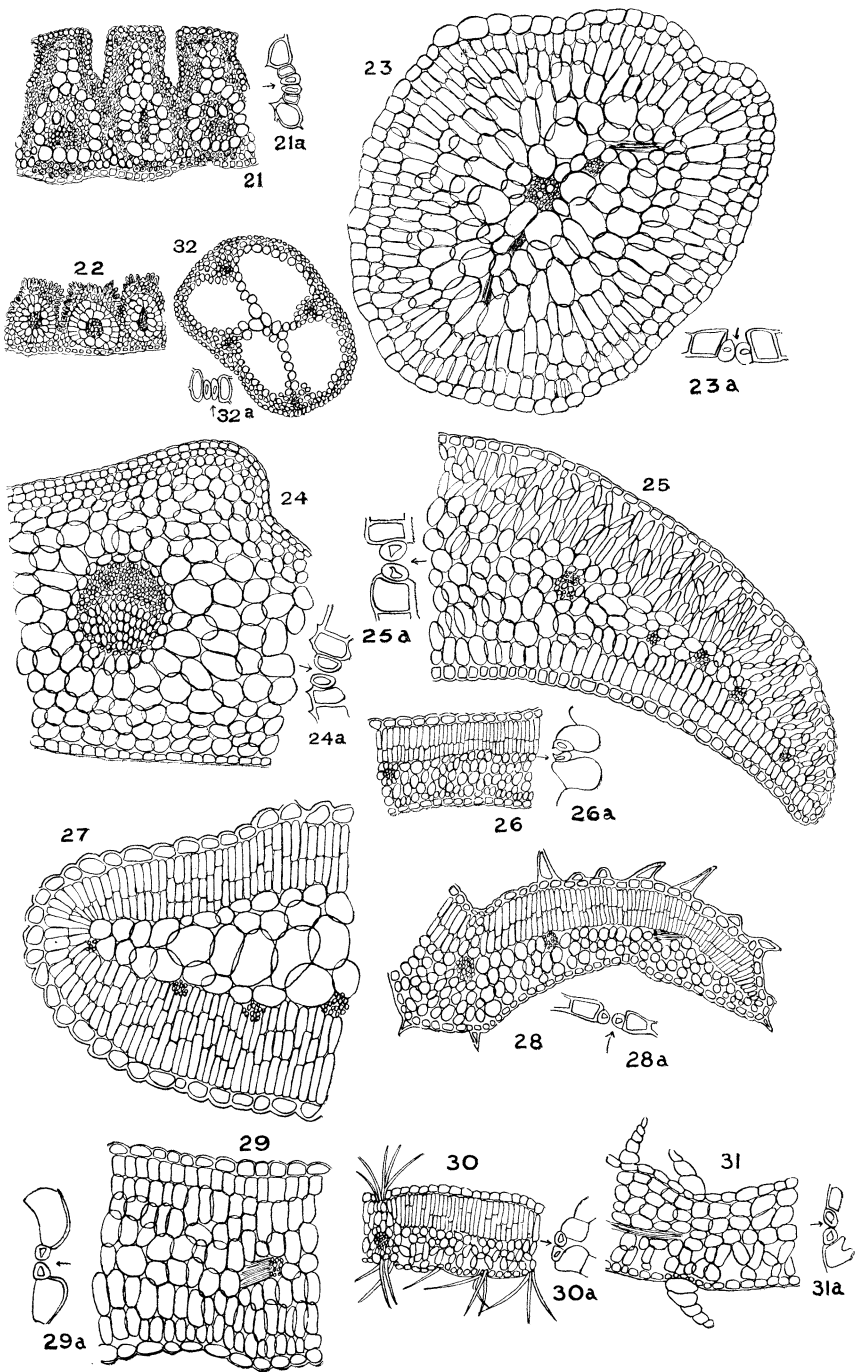


FIG. 4.





species of Bermudan plants with relation to the environmental factors of the sand dunes upon which the plants grew. In this paper a short bibliography of the principal papers is given.

EXPLANATION OF THE PLATES.

In Plate II, Fig. 1, is shown the frontal sea dune at Sea Side Park covered with the marram grass *Ammophila arenaria* and a large clump of *Cakile edentula*, while in Fig. 2 is represented the crest of the frontal dune covered with marram grass, back of which occur the waxberry *Myrica carolinensis* and the clumps of *Hudsonia tomentosa*.

The photograph reproduced in Plate III, Fig. 3, represents the thicket formation at South Sea Side Park composed of *Ilex opaca*, *Sassafras officinale*, *Rhus radicans* and *Solidago sempervirens*. In Fig. 4, Plate III, is represented a slough with floating rafts of *Eleocharis pygmaea*. The twenty enlarged figures with details of stomata, shown in Plate IV, represent the structure of the leaves of the sand strand plants of New Jersey, while the twelve figures and stomata enlargements represent the leaf structure of typic salt marsh species (Plate V).